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This Week's Citation Classic ®

Chitty D. Population processes in the vole and their relevance to general theory. *Can. J. Zool.* 38:99-113, 1960.
[Bureau of Animal Population, Department of Zoological Field Studies, Oxford University, England]

On the assumption that vole populations are a special instance of a general phenomenon, I proposed that all species are capable of limiting their own numbers without destroying their resources or depending on enemies or bad weather to keep them from doing so. I suggested that with increasing numbers, individuals become more susceptible to local hazards, regardless of what they are and whether or not they are density-dependent. [The *SCI*® indicates that this paper has been cited in more than 205 publications, making it the most-cited paper from this journal.]

Vole Populations: A Model for Others?

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I had been invited to come over to Canada from Oxford to help set up the PhD program of a student, Charles Krebs. Also, I was being considered as a future member of the Department of Zoology at the University of British Columbia in Vancouver. Had I known this, I would have been more circumspect in replying to a vote of thanks given by the head of the department. I would not have joshed him about the profound sleep he went into during one of my talks. Despite this solecism, I was offered the job, accepted it, and went from being a full-time research worker to an almost full-time lecturer.

I was able to make this switch because Krebs[1] had found populations of lemmings at Baker Lake, Northwest Territories, behaving much like populations of voles at Lake Vyrnwy, Wales. Despite differences in habitat, both observations seemed to have a common explanation, which Krebs was already testing. Instead of studying variables that differ from place to place, I maintained, we should study the behavior of the animals themselves and see how it affects their probability of survival. Terminal fates would then be of purely local interest.

The process I had in mind was analogous to senescence. Old animals differ physiologically from young ones and are likely to die faster, even when both are living under the same constant environmental conditions. I argued that individuals born in crowded populations differ congenitally from those born in increasing populations and that the effects of independent variables, such as weather, become more severe as numbers rise and quality falls.

There's something to the idea of qualitative change, but probably not to the suggested process of deterioration. Indeed, the evidence against it was lying dormant in results already gathered by Janet Newson and me,[2] for when we got around to our analysis, we decided that disappearing voles were physiologically sound. The disruptive change seemed to be in behavior.

Self-regulation can no longer be dismissed as one of the ways in which numbers are determined throughout the animal kingdom; weather cannot be assumed to act independently of density; and purely local causes of death may be irrelevant to general statements about the regulation of population density. These views are arguable; but a view I regarded as unarguable is that all explanations must be tested experimentally. The need for controls is often overlooked in population ecology.

A sine qua non for an experimental approach is to compare instances of the phenomenon with appropriate instances from which it is absent; we limit ourselves to explaining differences between multifactorial systems we can't understand in their entirety. Unfortunately, the search for consistent *differences* between complex events is sometimes misrepresented as an attempt to explain *events themselves* in terms of single factors.[3]

The experimental search for necessary conditions avoids most of the semantic controversies with which population ecology continues to be plagued; but this paper did little to shake the simple faith of many ecologists in the explanatory power of long-term descriptive studies.[4] Nor did it discourage others from trying to settle difficult questions by appeals to reason instead of experimentation.[5] But it did set the stage for a new generation of studies on cycles in numbers of small mammals.[6]

1. Krebs C J. *The lemming cycle at Baker Lake, Northwest Territories, during 1959-1962.* Tech. paper. No. 15, Arctic Institute of North America, 1964. 104 p.
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3. Hilborn R & Stearns S C. On inference in ecology and evolutionary biology: the problem of multiple causes. *Acta Biotheor.* 31:145-64, 1982.
4. Chitty D. What regulates bird populations? *Ecology* 48:698-701, 1967.
5. Warkowska-Dratnal H & Stenseth N C. Dispersal and the microtine cycle; comparison of two hypotheses. *Oecologia* 65:468-77, 1985.
6. Tait M J & Krebs C J. Population dynamics and cycles. (Tamarin R H, ed.) *Biology of New World Microtus.* Spec. Publ., No. 8. Amer. Soc. Mammal., 1985. p. 567-620.

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